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THE FORMATION OF CLONAL TERRITORIES IN EXPERIMENTAL POPULATIONS OF THE SEA ANEMONE *ACTINIA TENEBROSA*

DAVID J. AYRE[1]

Department of Zoology, University of Western Australia, Nedlands, Western Australia, 6009, Australia

Abstract

Fine and gross-scale clumping of electrophoretically identical anemones (genotypic clumping) was detected 11 months after multi-clonal groups of adults had been transplanted into rock pools on two shores. The locomotory separation of non-clonemates following conflicts appeared to be the primary cause of gross-scale genotypic clumping of adults, and the fine-scale genotypic clumping of adults and recruits. The gross-scale clumping of adults and recruits must reflect the effects of localized asexual recruitment. In contrast, genotypic clumping was not detected within a third population with lower recruitment, located on a relatively smooth shore. In that population, adults were typically restricted to small individual depressions and movement was rarely detected. These data support the hypothesis that intergenotypic aggression may play an important role in determining the genotypic structure of populations, and indicate that the importance of this factor may be partially determined by the topography of the shore.

Introduction

Within several species of sea anemones, interclonal aggression is thought to play a major role in the formation of clonal aggregations (Francis, 1973a, b; Purcell, 1977; Sebens, 1982; Ayre, 1983a). Laboratory trials (Francis, 1973b; Ayre, 1982) and field observations (Ottaway, 1978) have shown that intraspecific aggression leads to the locomotory separation of adult anemones. Nevertheless, the importance of aggression in the field has chiefly been inferred from observations of seemingly static clonal boundaries. The most striking examples have been documented for the fissiparous *Anthopleura elegantissima,* where anemone-free zones have remained between clones for periods of up to four years (Francis, 1973a). However, in these cases it has not been possible to separate the effects of aggression from those of other factors, such as passive growth and dispersal, which may determine clonal distributions. Furthermore, the role of aggression has been obscured by recent reports that aggressiveness may be reduced or absent in pairs of non-clonemate *Metridium senile* of different sex (Kaplan, 1983) and for pairs of non-clonemate *M. senile* (Purcell and Kitting, 1982) and *Anthopleura xanthogrammica* (Sebens, 1984) within genetically diverse aggregations.

Actinia tenebrosa is an asexually viviparous, solitary species which is also believed to reproduce sexually, producing widely dispersed, genetically diverse colonists (Black and Johnson, 1979; Ayre, 1983a; 1984a). *A. tenebrosa* is dioecious (Ottaway, 1979) and it appears likely that each clone is unisexual (Ayre, 1984c). The majority of recruits into natural populations on stable rock platforms are the asexually produced

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[1] Present address: Department of Biology, University of Wollongong, P.O. Box 1144, Wollongong, N.S.W. 2500, Australia.

juveniles of resident adults (Black and Johnson, 1979; Ayre, 1983a). Brooded juveniles may settle at least several meters from their brood parents and consequently, local populations typically consist of at least several intermingled clones (Ayre, 1983a, 1984a, b). Nevertheless, clones may have restricted (clumped) distributions and it has been suggested that interclonal aggression is used to maintain and extend clonal territories (Ayre, 1983a). Adult *A. tenebrosa* fight using specialized nematocyst-bearing structures called acrorhagi (Ottaway, 1978). These can be used to attack adult or juvenile non-clonemates within tentacle contact (Ayre, 1982). Each fight may last for as little as a few minutes. In some cases acrorhagial scarring persists and is visible for several days. In the field, resident adults are most often able to repel adult immigrants (Ottaway, 1978). In the laboratory, even mild attacks may significantly increase the level of juvenile mortality (Ayre, 1982).

This paper documents the active behavioral formation of clumps of genotypically identical anemones within experimental populations of *A. tenebrosa* and provides an indirect test of the hypothesis that intergenotypic aggression is directed only against non-clonemates of the same sex.

Materials and Methods

Experimental design

All experiments were conducted on exposed, sloping limestone shores within three natural populations of *A. tenebrosa* on the coast of Rottnest Island, Western Australia (32°S; 115°30E). All adult anemones (≥10 mm column diameter; Ayre, 1984b) were found within a band of shore approximately 1 m high, in the lower and mid-intertidal zone. The experimental sites were on shores of two topographic types. Two sites were within areas of small rockpools on shores at Green Island and Salmon Point. Pools ranged up to 70 cm in diameter and some individual pools contained more than 50 adults. The third site was an area of smooth shore within one of three populations at Strickland Bay (Ayre, 1983b). These adults were typically isolated within small depressions (2 to 3 cm diameter).

To test the hypothesis that the formation of clumps of genotypically identical adult *A. tenebrosa* has a behavioral basis, multi-clonal groups of 40 adults were haphazardly transplanted onto each of twenty-seven 1-m long strips of shore. This was a reciprocal transplantation experiment in which adults were transplanted within and between the three populations (Ayre, 1985). Three study sites were established within each population, and at each site a 1-m strip of shore was allocated to anemones from each of the three populations. Transplants were performed in early November 1980, following the removal of all resident anemones from each of the 27 transplant strips. All adults were transplanted into the zone from which anemones had been removed, but were never intentionally returned to their original positions. All transplanted adults rapidly attached themselves to the limestone shore and all were in place for at least one hour prior to exposure to wave action. Detailed topographic maps, based on sketches and photographs, were prepared for each strip. To ensure that the transplanted adults could be distinguished from recruits that had grown to >10 mm (new adults), the locations and sizes of all transplanted adults, new adults, and juveniles were monitored at approximately two-month intervals. After 11 months the positions of all surviving adults and new recruits were recorded and all anemones were then collected. Adults were stored, live, at 4°C for up to five days prior to dissection, and adults and all juveniles were then stored at −20°C pending electrophoresis. The sexes of adults were determined on the basis of the color and morphology of their gonads (Ayre, 1984b).

Electrophoresis

All anemones were assayed for the five polymorphic enzymes catalase (CAT, EC 1.11.1.6), malate dehydrogenase (MDH, EC 1.11.1.37), mannose phosphate isomerase (MPI, EC 5.3.1.8), phosphoglucomutase (PGM, EC 2.7.5.1), and superoxide dismutase (SOD, EC 1.15.1.1), as described by Ayre (1983a). Anemones were considered to be non-clonemates if they had different genotypes at one or more loci. Electrophoretically identical anemones might be either clonemates or non-clonemates.

Analysis

Clumping of electrophoretically identical (genotypic clumping) anemones was examined on two spatial scales (Ayre, 1983a). Within each population, fine-scale genotypic clumping, on a scale consistent with the predicted effects of intergenotypic aggression, was tested by comparing the proportions of anemones with only genotypically identical neighbors within a two-cm radius (*i.e.*, within tentacle contact; Ayre, 1982) and a 2–4 cm radius. It was assumed that if aggression was occurring then a disproportionate number of near neighbors should be electrophoretically identical. Gross-scale genotypic clumping within each whole transplant strip, resulting from differential dispersal or mortality, was tested for by comparing the mean distances between all pairs of electrophoretically identical anemones and all pairs of electrophoretically different anemones. This analysis was conducted for each multi-locus genotype represented by two or more anemones. Genotypes were considered to be clumped if the mean distance between pairs of anemones with that genotype was less than the mean distance between them and all other anemones. These results were then pooled for all strips within each population, and the proportions of clumped and unclumped genotypes were compared with the expectation that half of all genotypes would have clumped distributions due to chance alone. These tests for genotypic clumping should be conservative since it may not be possible to distinguish all clones using only five variable loci and the areas of the transplant strips may be small relative to the limits of juvenile dispersal.

Results

Survival and recruitment

At the conclusion of the experiments, the mean numbers ($\bar{x} \pm$ S.E.) of surviving adults per strip were similar within each of the three populations ranging from 17 $\pm$ 2 at Strickland Bay and Salmon Point, to 21 $\pm$ 2 at Green Island. As was expected, all adults were restricted to the shelter of pools and depressions whereas many juveniles settled on exposed shore (Fig. 1). Settlement and recruitment varied considerably within and between colonies, and 445, 187, and 51 recruits were collected from Green Island, Salmon Point, and Strickland Bay, respectively.

Fine-scale genotypic clumping

Genotypic clumping on a scale consistent with the predicted effects of intergenotypic aggression was detected on the rough shore within both the Green Island and Salmon Point populations (Table I). Disproportionately more anemones had only genotypically identical neighbors within a 2 cm radius compared with the proportions within a 2- to 4-cm radius. Significant levels of fine-scale clumping were detected within the groups of transplanted adults collected from Salmon Point and within the groups of transplanted adults and recruits collected from both Green Island and

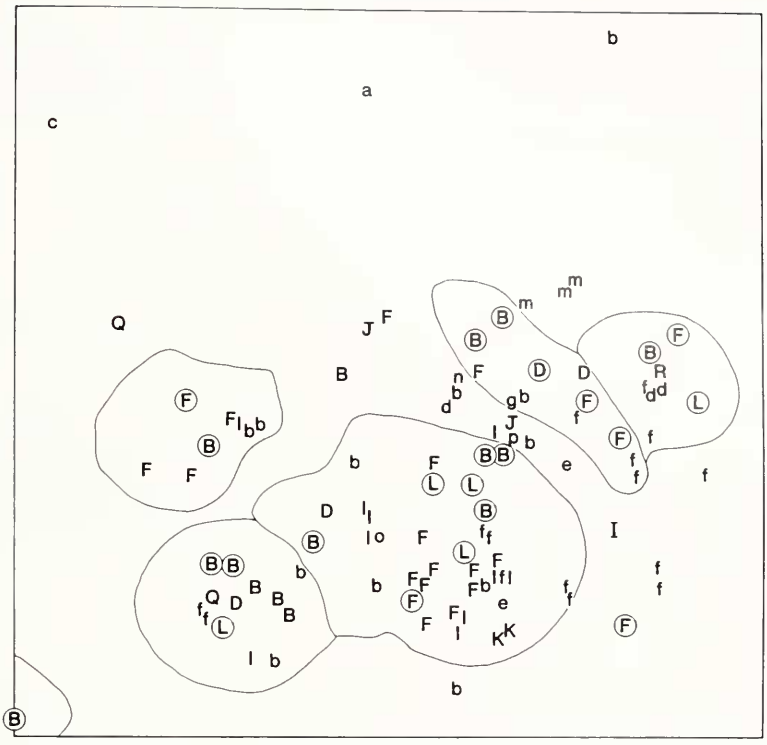

FIGURE 1. The distribution of all adult and juvenile *Actinia tenebrosa* 11 months after a multi-clonal group of 40 adults had been transplanted haphazardly into rock pools (outlines shown as lines) on a 1-meter wide strip of shore at Green Island. Each anemone is represented by a letter denoting its size and age, and 5-locus genotype. A total of 18 different genotyopes are represented. This strip was chosen at random from the set of 27 experimental sites. Transplanted adults = enclosed upper case letter; adult recruits = upper case letter; juvenile recruits = lower case letter.

Salmon Point (Table I). In contrast there was no such clumping of electrophoretically identical adults at Strickland Bay. In fact, a greater proportion of anemones had electrophoretically different neighbors within a 2-cm radius as compared with a 2- to 4-cm radius (Table I), although this difference was not statistically significant. There was some evidence of fine-scale genotypic clumping of transplanted adults and recruits at Strickland Bay, however these data provided only a weak test for such clumping as only 10 recruits were found within 4-cm of transplanted adults (Table I).

Gross-scale genotypic clumping

Each of the 27 transplant strips was found to support anemones with at least 3, and typically 5 or more, 5-locus genotypes. Genotypes were intermingled on the shore, and many juveniles were detected outside the limits of adult distributions (Fig. 1). Nevertheless, for transplanted adults, a significant majority of genotypes were judged to be clumped within the Green Island and Salmon Point strips (Table II), although these results were not statistically significant for either individual population. In contrast only half of the 45 groups of genotypically identical adults on the smooth shore at Strickland Bay were judged to be clumped, the proportion expected

TABLE I

Comparison of the numbers of adult Actinia tenebrosa *with only genotypically identical adult neighbors*[a] *(S) or at least one genotypically different neighbor (D) within a 2-cm and 2 to 4-cm radius*

		Separation					
		<2 cm		2 to 4 cm			
Population	Pairing	S	D	S	D	$\chi^2_{(1),1}$	*P*
Green Island	Adult-adult	18	12	17	28	2.74	<0.05
Green Island	Adult-recruit	65	28	32	68	26.2	<0.001
Salmon Point	Adult-adult	19	4	13	17	6.83	<0.005
Salmon Point	Adult-recruit	14	13	5	21	7.62	<0.005
Strickland Bay	Adult-adult	12	21	15	12	1.50	N.S.
Strickland Bay	Adult-recruit	5	0	2	3	Fisher's Exact Test	0.083

Comparisons are made for pairs of transplanted adults, and transplanted adults and adult and juvenile recruits. Data are presented for anemones within three experimental populations, which had been established 11 months earlier by haphazardly transplanting multi-clonal groups of 40 adult anemones onto cleared areas of shore.

[a] Based on 5 locus-genotype.

N.S. $P > 0.05$.

by chance alone (Table II). In addition, at Green Island, a significant majority of the groups of electrophoretically identical transplanted adults and recruits were judged to be clumped (Table II, $P < 0.001$). In contrast only half of such groups were clumped within the Salmon Point and Strickland Bay populations (Table II), however, this may reflect the underlying unclumped distribution of genotypes represented by transplanted adults. Furthermore, the present experimental design provides only a weak test for gross-scale genotypic clumping involving recruits since each test was restricted to only a 1-m^2 experimental strip. In natural populations juveniles may be dispersed passively over several meters and genotypic clumps are often spread over at least several square meters of shore (Ayre, 1983a). Therefore, this difference between populations may be a real environmental effect but cannot be considered evidence that the same processes do not operate on all three shores.

Effects of sex

The distribution of the 59 pairs of electrophoretically distinct sexually mature adults separated by ≤4 cm did not support the hypothesis that aggression is directed only towards non-clonemates of the same sex. The proportions of electrophoretically different, same-sex and mixed-sex pairings separated by <2 cm and 2–4 cm were not significantly different (Table III). This implies that if intergenotypic aggression is a major determinant of the distribution of genotypes on these shores then the initiation of conflicts is not affected by similarity of sex.

DISCUSSION

The rapid formation of genotypic clumps within experimental populations of adult *A. tenebrosa* supports the hypothesis that clonal distributions may be, at least partially, determined by the effects of interclonal aggression and subsequent migra-

TABLE II

The incidence of gross genotypic[a] *clumping within experimental groups of* Actinia tenebrosa *in each of three populations*

Group	Population	Genotype			
		Clumped	Not-clumped	$\chi^2_{(1),1}$	
Transplanted adults	Green Island	18	11	N.S.	
	Salmon Point	15	7	N.S.	
	Strickland Bay	23	22	N.S.	
Transplanted adults and recruits	Green Island	50	19	13.04	<0.001
	Salmon Point	23	22	N.S.	
	Strickland Bay	12	14	N.S.	

Data are presented for adult anemones which had been haphazardly transplanted 11 months prior to sampling, and for those adults and all adult and juvenile recruits. Chi-squared analyses were used to determine if a significant majority of genotypes were clumped.

[a] For each 5-locus genotype, anemones were judged to be clumped if the mean distance between all anemones with that genotype was less than the mean distance between all anemones with different genotypes.

N.S. not significant $P > 0.05$.

tion (Ayre, 1983a). Similarly, genotypic clumping has been described within natural populations of *A. tenebrosa* (Ayre, 1983a) where interclonal conflicts have been observed. These findings, together with experimental demonstrations that these clones are locally adapted (Ayre, 1985), support the theoretical prediction that inter-clonal competition should restrict clones to those parts of the habitat to which they are best adapted (Williams, 1975).

In this study both fine and gross-scale genotypic clumping developed within at least some of the multi-clonal groups of adults which had been established 11 months earlier by haphazard transplantation. Genotypic clumping on both scales is most simply explained by the differential migration of genotypes following interclonal conflicts, or by the preferential association of clonemates. Fine-scale clumping of adults occurred on a scale that was consistent with the predicted, aggressive repulsion of non-clonemate near neighbors. Disproportionately more pairs of anemones within

TABLE III

Comparison of the numbers of pairs of genotypically different[1] *adult* Actinia tenebrosa *with the same or different sex which were separated by <2 cm and 2 to 4 cm*

Pairings	Separation		
	<2 cm	2 to 4 cm	
Same sex	8	15	$\chi^2_{(1),1} = 0.32$
N.S.			
Male-female	10	26	

Results were pooled for groups of anemones which had been haphazardly transplanted into 3 populations 11 months prior to sampling.

[1] Based on 5 locus-genotype.

N.S. $P > 0.05$.

the range of tentacle contact were genotypically identical than those just outside the range of contact (2–4 cm). Such fine-scale genotypic clumping could also be explained by the differential migration of adult clonemates into favored micro-habitats, but this seems inconsistent with the overlapping gross-scale distribution of genotypes detected in this study (Fig. 1) and within natural populations (Ayre, 1983a). Gross-scale genotypic clumping on rough shores could have resulted from the aggressive repulsion and subsequent migration of non-clonemates, differential migration of genotypes into particular microhabitats, or differential mortality of clones within microhabitats. It is not possible to distinguish between the first two hypotheses. However, the third hypothesis is weakened by the fact that, although mortality rates were similar in each population, no evidence of gross genotypic clumping was detected at Strickland Bay. At Strickland Bay pedal locomotion is severely restricted by the topography of the shore, since anemones are almost all restricted to small, individual pools. As might be predicted, because adult anemones on that shore were rarely within tentacle contact, no intraspecific fighting was observed or acrorhagial scarring detected during a three-year study of both the experimental and natural populations at that location. In contrast, 12 fights between pairs of adults were inferred from the presence of acrorhagial scarring during the present 11-month study of experimental populations at Green Island and Salmon Point. In eight of these cases one adult in each pair died or was lost from the study site within the following two months, which may be compared with an average of 7% mortality per 2-month period for all adults in this experiment (Ayre, 1985).

At Green Island, statistically significant gross-scale genotypic clumping of transplanted adults and adult and juvenile recruits was superimposed upon the already clumped distributions of the groups of transplanted adult clonemates. This result strongly supports the prediction that, within natural populations, clonal territories are extended by the combined effects of interclonal aggression and the passive dispersal of asexually produced juveniles (Ayre, 1983a). Passive dispersal should always play a major role in extending clonal boundaries. However, the fine-scale clumping of adults and juveniles, detected at Green Island and Salmon Point, supports the hypothesis that this effect may be strengthened by intergenotypic aggression (Ayre, 1983a). Such fine-scale genotypic clumping of adults and juveniles should be expected to develop on all types of shore as a result of attacks on juvenile non-clonemates which settle close to adults. Nevertheless, it is clear from this study and earlier work (Ayre, 1985) that environmental factors affecting populations can greatly influence the rate of expansion of clones through effects on asexual fecundity, recruitment, and the frequency of intergenotypic conflicts.

The conclusions of this and earlier studies of the genetic structure of populations of *A. tenebrosa* (Black and Johnson, 1979; Ayre, 1983a, 1984a, b) are in apparent contrast with the outcome of studies of the northern hemisphere species *Actinia equina* var mesembryanthemum. Several authors have claimed that in British populations there is little fine or gross-scale clumping of clonal genotypes and that asexually produced juveniles are in fact widely dispersed (Orr *et al.,* 1982; Quicke and Brace, 1983; Brace and Quicke, 1985, 1986a, b). The latter conclusion is based principally on the finding that single locus genotype frequencies approach the values predicted for Hardy-Weinberg equilibria, an outcome which is more consistent with the recruitment of sexually reproduced recruits. In addition, Brace and Quicke (1986b) have concluded that for *A. equina* the principal role of intraspecific aggression is "to act to enhance adult survivorship through the securement of space . . ." Although Brace and Quicke (1985) emphasize the apparent differences between populations of the two species, they recognize that in their studies environmental differences be-

tween sites may account for differences in the importance of both localized asexual recruitment and inter-genotypic aggression. In fact they conclude that in the single area in which genotypic clumping was detected anemones may have been less susceptible to dislodgement resulting from wave action. It could also be argued that only two of their four study sites contained anemones at sufficiently high densities (<2.5 cm mean nearest neighbor distance) to provide a meaningful test of the effects of inter-genotypic aggression, and that at least three of their study sites were too small (0.18–0.59 m^2) to provide a useful test for gross-scale genotypic clumping. This apparent contrast of life-history tactics may therefore simply reflect the decision to study populations of *A. equina* in which low levels of asexual recruitment and interclonal aggression are favored, and the use of different methods of analysis in the Australian and British studies. It is certainly true that interpopulation variation with respect to many life-history characters has been documented for other anemones, including the contributions of sexual and asexual reproduction to recruitment, as inferred from allozyme data, for *A. tenebrosa* (Ayre, 1984a) and *Metridium senile* (Hoffmann, 1986).

The present results do not support the idea that the aggressive response of adult *A. tenebrosa* to adult non-clonemates (Ayre, 1982) is reduced when pairs of adults are of different sex. Similar proportions of same sex and mixed sex pairs were detected within and immediately beyond the range of tentacle contact. Since only 59 suitable pairings were recorded, it is possible that similarity of sex may have some influence on the aggressiveness of pairs. This finding contrasts with Kaplan's (1983) clear demonstration that mixed sex pairs of *Metridium senile* would not fight. Sebens (1984) also failed to find any evidence that the incidence of aggression is affected by similarity of sex in populations of *Anthopleura xanthogrammica.* These results, together with other reports of variation in the sensitivity of histocompatibility reactions in coelenterates (Resing and Ayre, 1985) and the finding that factors such as age (Hidaka, 1985) and prolonged contact with non-clonemates may modify their expression (Purcell and Kitting, 1982; Sebens, 1984), highlight our limited understanding of these processes.

Although the sensitivity of the histocompatibility response has not been thoroughly tested for *A. tenebrosa,* it is clear that intergenotypic aggression plays an important role in determining the genotypic structure of populations of *A. tenebrosa* on some shores, where it must therefore play an important role in inter-clonal competition. The finding that genotypic clumping did not develop on the smooth shore at Strickland Bay implies that interclonal aggression accelerates and enhances the effects of passive asexual dispersal on the development of clonal territories. The reciprocal transplant study which generated the data described in the present study revealed that clones of this species were highly locally adapted. With regard to asexual fecundity, however, the importance of inter-genotypic aggression as a component of clonal fitness has not been determined. It seems likely that aggressiveness should be most strongly selected for on shores which support moderate or high densities of mobile adults.

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